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Thirty Years of Research in Kibale National Park, Uganda, Reveals a Complex Picture for Conservation

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Kibale National Park, Uganda, has a rich and abundant primate community and a complicated history of anthropogenic disturbance. Moreover, it has been the focus of over 30 yr of research and has received considerable attention from nongovernmental and governmental conservation organizations. As a result, Kibale serves as a valuable case study with which to evaluate the factors that regulate primate population density and the challenges of deriving generalizations for conservation. We review the impact of logging and forest fragmentation on primate population density and trace the efficacy of various conservation strategies. A 28-yr comparison of primate abundance in logged and unlogged forests and a 10-yr study of forest dynamics showed that primate recovery in logged areas is generally slow or not occurring at all for some species, which is likely driven by the fact that the forest is not recovering as expected. No primate species characteristic predicted their ability to live in forest fragments around Kibale. While a nutritional model was useful to predict the abundance of colobus in forest fragments outside of Kibale, a 5-yr study revealed that human land-use practices are more fundamentally shaping population dynamics. We evaluate data on primate abundance in light of Milton's protein/fiber model to predict colobine biomass. We demonstrate

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that while the model can predict colobus biomass in pristine habitats, the 2 colobus species respond differently to disturbance. We offer suggestions for future conservation research and consider strategies to conserve forested national parks based on experiences gained over 30 yr.

KEY WORDS: fragmentation; logging; colobus; population regulation; nutritional ecology.

INTRODUCTION

A fundamental issue in ecology is determining factors that regulate animal population density. (Boutin, 1990; Struhsaker, 1997). The importance of understanding determinants of animal abundance has increased with the need to develop informed management plans for endangered or threatened species. With respect to primates, these theoretical issues are critical because tropical forests occupied by primates are undergoing rapid anthropogenic transformation and modification (National Research Council, 1992). Cumulatively, countries with primate populations are losing *ca.* 125,000 km^2 of forest annually (Chapman and Peres, 2001). Other populations are being affected by forest degradation (logging and fire) and hunting. However, understanding and predicting factors that determine abundance of particular primate species has proven extremely difficult and new ways forward must be sought.

Kibale National Park in Uganda, has a rich and abundant primate community and a complicated history of anthropogenic disturbance. Moreover, Kibale has been the focus of >30 yr of research and has received considerable attention from nongovernmental and governmental conservation organizations. It thereby serves as a valuable case study with which to evaluate the factors that regulate primate population density and the challenges of deriving generalizations for conservation.

Our objectives are twofold. First, we examine the responses of the Kibale primate community to 2 types of anthropogenic disturbance, logging and forest fragmentation, and consider the value of a nutritional model to account for variation in colobine abundance. Second, we build on the experiences gathered by 2 generations of primatologists to evaluate the effectiveness of various conservation strategies. Struhsaker developed and managed a biological research station in Kibale for nearly 18 yr (1970–1988) and initiated many of the conservation plans that were adopted by the agencies managing Kibale (Ugandan Forest Department, Ugandan Wildlife Authority). Colin and Lauren Chapman began working in Kibale in 1989, Lambert in 1991, and all still work in the region. They have witnessed a shift in the nature of management tactics from ones largely based at the local level, to ones orchestrated at the national level and funded by large international donors.

In the concluding portion of the paper, we consider the biological and historical complexity of Kibale and suggest potential ways forward. We need to work towards understanding the factors that regulate animal populations; however, lessons from Kibale and elsewhere indicate that we should shift from seeking single, or simple causative models to considering multifactorial patterns. Also, because the time between quantifying biological interactions and implementing conservation tactics in light of the data is typically long scientific endeavors must be partially framed to provide information of immediate value for conservation planning. This need not entail intensive funding. Indeed, we argue that it is simply the long-term presence of committed personnel that is the most robust factor in determining success in forest conservation and management.

LOGGING, FOREST FRAGMENTATION, AND PRIMATE NUTRITIONAL ECOLOGY IN KIBALE

Site Description

Kibale National Park (766 km^2) is located in western Uganda near the foothills of the Ruwenzori Mountains (Struhsaker, 1975; 1997; Skorupa, 1988). The park consists of moist semideciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; Chapman and Lambert, 2000). Mean annual rainfall in the region is 1749 mm (1990–2001, or 1547 mm from 1903–2001); the mean daily minimum temperature is 14.87°C; and the mean daily maximum temperature is 20.18°C (1990–2001). There are distinct wet and dry seasons that are bimodal in distribution (Chapman *et al.*, 1999). Kibale is the home to 12 species of primates, 6 of which are diurnal and have been subjects of extensive research: red colobus (*Procolobus tephrosceles*), black-and-white colobus (*Colobus guereza*), red-tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*), and chimpanzees (*Pan troglodytes*; Struhsaker, 1997). The absence of hunting for several decades (Struhsaker, 1975) and the fact that primate biomass in Kibale is among the highest ever reported (Oates *et al.*, 1990; Fashing and Cords, 2000), results in a rich and abundant primate community, individuals of which are relatively easily located, habituated, and studied.

Logging

The most prevalent form of disturbed forest habitat with conservation potential is selectively logged forest (Frumhoff, 1995; Struhsaker, 1997).

Although researchers have examined the effects of selective logging on primate populations, the majority have been limited by methodological shortcomings. Studies conducted soon after logging has occurred (Plumptre and Reynolds, 1994; Bennett and Dahaban, 1995; Ganzhorn, 1995) may produce a biased perspective because they do not account for lag time between disturbance and habitat loss (Brooks *et al.*, 1997; Cowlishaw, 1999) and anthropogenic disturbance lowers recruitment, but does not usually kill primates (Struhsaker, 1997). Most other researchers have not had data on primate abundance before and after logging and thus use neighboring unlogged sites to contrast to the logged site; the study of Grieser-Johns and Grieser-Johns, (1995) is an exception. The approach suffers by not taking into account natural variation in primate abundance within undisturbed forest (Johns, 1986; Chapman and Chapman, 1999).

While not having before and after data, we attempted to avoid these shortcomings by comparing primate abundance over a 28-yr period in unlogged forest and over a 17-yr period in logged areas, to test the expectation that primate populations would increase in the logged areas over time (Chapman *et al.*, 2000). Overall, we conducted 214 census walks over 837 km. All species showed no change in group density in the unlogged forest between the censuses, except blue monkeys which declined (Figure 1). In the lightly logged forest, mangabeys had marginal increases in group density between the 1980 and 1997 censuses. All other species showed no change in density between 1980 and 1997. In the heavily logged forest, *Colobus guereza* showed a marginal increase in group density between 1980 and 1997, while red-tailed monkey and blue monkey populations declined between the 2 periods. Mangabeys showed no change in group density between 1980 and 1997 within the heavily logged area. The changes in density reflect pattern differences noted at each time among forestry compartments (Figure 1; Chapman *et al.*, 2000).

We also examined changes in abundance over time considering relative abundance (groups seen per km walked; Chapman *et al.*, 2000). The index removes variance in estimating distances among observers at different times and is a valuable comparative tool (Mitani *et al.*, 2000). The index suggests that in the heavily logged area all of the species, except mangabeys, have declined in abundance between 1980 and 1997 (Chapman *et al.*, 2000). However, unlike group density estimates, the index also suggests that red colobus have declined in the unlogged and lightly logged areas over this time.

Two intriguing questions arise from our research: 1) why are the 2 guenon species declining in abundance in the logged area when general forestry principles suggest the forest should be recovering and 2) why do they respond differently to logging? Detailed examination of forest

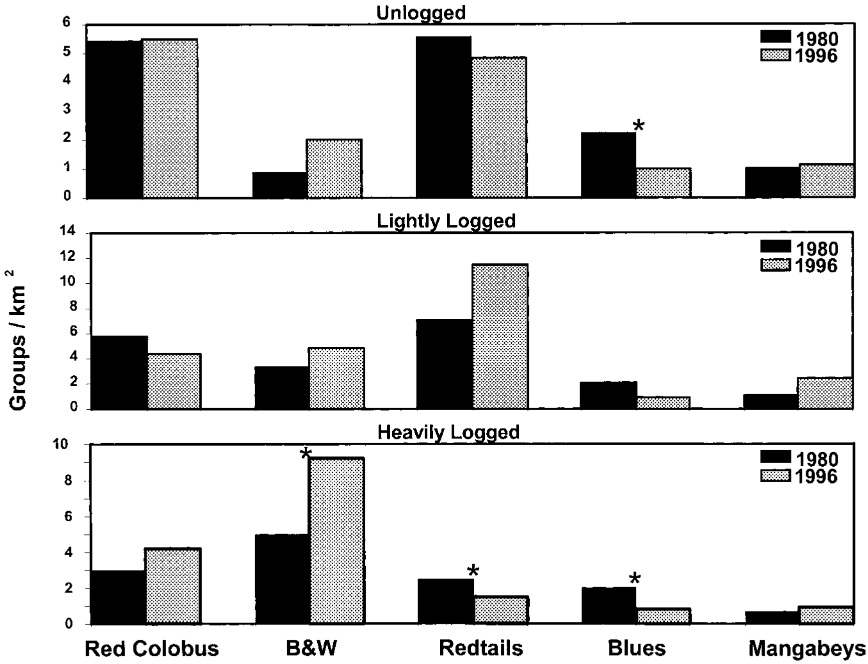

Fig. 1. Mean group densities for primate species in the unlogged, lightly logged, and heavily logged forest of Kibale National Park, Uganda for 2 periods (1980–1981, and 1996–1987). *indicates significant differences over time. In 1980–1981, densities of *Procolobus tephrosceles* and *Cercopithecus ascanius* were lower in the heavily logged area versus the lightly or unlogged areas and density of *Colobus guereza* differed among all areas. In 1996–1997, density of *Colobus guereza* still differed among all areas and density of *Cercopithecus ascanius* was lower in the heavily logged area versus the lightly or unlogged areas (Chapman *et al.*, 2000).

structure over the last decade provides some insight into these questions. It is often assumed that the gaps created by logging increase light reaching forest floor or subcanopy, which in turn accelerates growth of existing trees (Fox, 1976; Putz *et al.*, 2000). In a 10-year study, we quantified tree community dynamics in selectively logged areas harvested at different intensities and compared their recovery to 2 unlogged areas in Kibale (Chapman and Chapman, 2004; Chapman and Chapman, 1997). Over the 10 yr, 527 of the original 4840 tagged trees (≥10 cm DBH) died; the mortality rate was highest in the heavily logged area. The density of new trees varied significantly among areas: it was highest in the lightly logged area, but the density of new recruits in the heavily logged area did not differ from those in unlogged areas. Overall, as expected the more heavily logged areas had higher growth rates than the unlogged or lightly logged areas. However, there is no difference among areas in the magnitude of change in basal area as more trees died in the heavily logged area; and in both 1990 (>20 yr post-harvest) and 2000 the basal area in the heavily logged area was less than those of the unlogged areas.

In general, findings from the heavily logged area indicate that the expectation that regeneration will be accelerated in logged areas relative to unlogged areas was not met. Elephants, dense herbaceous vegetation, and the characteristics of the pioneer tree community all likely contribute to the slower than expected recovery (Struhsaker *et al.*, 1996; Chapman *et al.*, 1999; Chapman and Chapman, 1999; Paul *et al.*, in press). Elephants use forest gaps more than closed-canopy forest and large gaps, such as those created by logging, more than small ones (Struhsaker *et al.*, 1996). Elephant use of an area and damage to young trees is directly related to the density of herbaceous vegetation (Struhsaker *et al.*, 1996).

Fragmentation

As deforestation and habitat fragmentation accelerate throughout the tropics, the survival of many forest primates depends largely on their ability to cope with such changes. Historically the region in which Kibale is located, the Toro District, was noted for its extensive forest and abundant big game (Naughton-Treves, 1999). Historians describe Western Uganda's forests as sparsely populated before the 20th century (Osmaston, 1959; Naughton-Treves, 1999). In the Game Department archives of 1934, (p. 319), it is stated that "The Toro district is the most difficult of the control areas and will be hard work for many years to come. There are some thirty to forty herds of elephant totaling fully 2000 animals, the majority of which live in close proximity to settlements and cultivation. This is only made possible owing to the appalling nature of the country and the density and height of the grass." Where there were once isolated agricultural settlements amidst wildlife habitat, today there are small islands of wildlife habitat embedded in an agricultural landscape (Naughton-Treves, 1999).

In 1995 we censused 20 forest fragments that had existed for several decades near Kibale (Onderdonk and Chapman, 2000). For each fragment we determined the presence or absence of all diurnal primate species and population sizes of black-and-white colobus. Our objective was to test pre-existing generalizations regarding animal traits permitting species to persist in fragments. For example, home range size has frequently been cited as a factor influencing the ability of primates to live in fragments (Estrada and Coates-Estrada, 1996; Lovejoy *et al.*, 1986). In contrast to these generalizations, no specific characteristic, including home range size, body size, group size, or degree of frugivory, predicted the ability of species to live in forest fragments. Furthermore, no patch characteristic, including area, distance to the nearest patch, distance to Kibale, or number of food trees present, predicted the presence of a particular species in a fragment.

Five years after the initial survey, we recensused the same fragments and discovered that of the 16 fragments inhabited by primates in 1995, 3 had been largely cleared and resident primate populations were no longer there. We documented population declines and lowered fertility rates in the remaining fragments for some species. For example, black-and-white colobus populations declined from 165 individuals in 1995 to 118 in 2000 and the number of infants per female declined from 0.405 to 0.026. In contrast, red colobus groups occupied 7 fragments during the initial survey and 11 fragments in 2000. In the 2000 census, we counted 159 red colobus and the ratio of infants to adult females was 0.25. Why the 2 colobine species appear to respond differentially to living in fragments is an intriguing puzzle.

Much of the previous work on primates in fragmented habitats has involved fragments protected from human use (Tutin *et al.*, 1997; Laurance *et al.*, 2002). In reality, most fragments are not protected; they are on land managed by private citizens who depend on them for fuelwood, medicinal plants, or game. While studies in protected reserves have provided us with many insights, they may have biased our perception of the value of forest fragments to primates. While the fragments outside of Kibale have been intact as least since the 1940s, local sociopolitical conditions and human population density have changed and fragments are now being cleared rapidly. It seems the incentive to clear fragments is based on changing economics; most areas were cleared for the production of charcoal, gin, bricks, or timber. All of these products can now be sold to the capital city since the road has improved (construction was mostly completed in 2000). In 5 yr, 19% of the surveyed fragments near Kibale were cleared to the extent that they no longer support primates. If this level of clearing remains constant, all fragments will be cleared in 26 yr. To reverse present trends would require a major conservation effort on a scale and of a nature that is not typically done.

Protein-to-Fiber Model

There have been few direct tests of general hypotheses proposed to account for variation in primate abundances. Notable exceptions are studies of folivorous primates. Milton (1979) proposed that the protein-to-fiber ratio is a good predictor of leaf choice (Milton, 1982, 1998; Milton *et al.*, 1980). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several researchers found positive correlations between colobine biomass and this index of leaf quality in populations separated by thousands of km (Waterman *et al.*, 1988; Oates *et al.*, 1990; Davies, 1994). We showed that the relationship also applies to small spatial scales and predicted the biomass of neighboring colobine population inside Kibale (Chapman and Chapman, 2002; Ganzhorn, 2002). We also tested the protein-to-fiber model via the forest fragments for which we could verify that colobus populations were stable and the forest had not changed (Chapman *et al.*, 2004). While we had initially hoped that 10–15 of the 20 fragments monitored in 1995 would be stable, we found that only 5 had populations that had not changed or whose fragment had not been seriously degraded. While disheartening from a conservation perspective, it still allowed for a test of the protein-to-fiber model. The biomass of colobus in the stable fragments could be predicted from the protein-to-fiber ratio of the dominant tree species in the fragments ($r^2 = 0.730$, $P = 0.033$). By combining our new data with previously published data (Oates *et al.*, 1990; Chapman and Chapman, 2002; Chapman *et al.*, 2002), we demonstrated that colobine biomass at the 14 sites could be predicted from the protein-to-fiber ratios of the mature leaves there ($r^2 = 0.869$, $P < 0.001$).

It is somewhat surprising that researchers have been repeatedly able to predict colobine biomass with the protein-to-fiber model. This trend is particularly surprising considering the inadequacies of census methodology and the fact that researchers are measuring the protein-to-fiber ratio of mature leaves, and colobines rarely eat mature leaves. In the sample of leaves from Kibale we found that the protein-to-fiber ratio of mature leaves and young leaves are strongly correlated ($r = 0.837$, $P < 0.001$), which suggests that measuring nutritional quality of mature leaves provides a reasonable index of the quality of young leaves, which are favored food items of many colobines.

Unfortunately, additional observations confound the application of the protein-to-fiber model to conservation planning. For example, our census data indicate that over time the 2 colobine species differ in their densities, relative abundances, and rates of population increase in response to selective logging despite the fact that the colobus biomass can be predicted by the protein-to-fiber ratios of potential foods at sites within the park (both species). Accordingly, factors other than, or in addition to, the ratio of protein-to-fiber are influencing population density. Data on population density in fragments are likewise difficult to interpret in light of the protein-to-fiber model. For example, while black-and-white colobus populations declined over a 5-yr period, red colobus numbers increased (as indicated by the number of fragments occupied) despite the fact that fragments have been degraded over the last 5 yr. Because the fragments have existed for decades, it is unlikely that they are just being colonized by the red colobus. Possibly population density is being influenced by additional factors that interact with nutrition (Milton, 1996).

REVIEW OF THE EFFECTIVENESS OF KIBALE CONSERVATION STRATEGIES

Scientists at academic institutions have traditionally contributed to conservation efforts by either providing information or by educating people and thereby increasing public awareness and interest. Indeed, data garnered from basic research are increasingly incorporated into decisions about protection and management of species. A majority of research projects are undertaken within a short time. There are, however, circumstances in which research has been conducted over a long enough period to provide a historical perspective on the efficacy of a variety of conservation schemes. Under these circumstances, academics are uniquely positioned to evaluate the conservation strategies. One way to view management schemes proposed for primate conservation is that they represent simple, typically nonreplicated, quasiexperiments set under a constantly changing social, economic, and cultural backdrop. Researchers who have a long-term presence at a particular site, such as Kibale, can provide an evaluation of which strategies were successful and which were not.

Struhsaker (2002) presented his ideas for effective park management based on nearly 18 yr in Kibale. Here, our aim is not to provide a repetitive review, but instead to comment on strategies whose effectiveness became apparent since the 1970–1988 period. In addition, we comment on strategies adopted since 1988.

Early on the Kibale project was provided 2–3 game guards with the authority to arrest poachers. The Kibale project supervised them, assisted with logistical support and paid a bonus for every poacher arrested, for every panga (machete), spear, net snare, gun, saw, and piece of confiscated timber brought in. The bonus was *ca*. 20% below the market value to discourage production or purchase of the items for profit by the guards. The annual cost of the bonus system in the 1980s was <$500. The system broke down in the early 1990s. Shortly thereafter, it is our impression that there was a dramatic increase in the number of snares. The simple and inexpensive system seemed to have been very effective to decrease pressure on the wildlife in Kibale.

In mid 1980s, the Kibale project started an education program that involved field trips, discussions with teachers and pupils, and ample opportunities for children from the neighboring community to come to Kibale.

At Kibale, children interacted with researchers, learned about ecology and forest biology, and, in general learned to view the Kibale project positively. Struhsaker (2002) did not evaluate the effectiveness of the program because he viewed that not enough time and effort was invested in the strategy to yield tangible results. However, the program was continued until 1993. Unfortunately, no formal evaluation it was attempted. However, it is our impression that it was very effective to shape attitudes of local villagers. The program emphasized communicating with young children. Today they are men and women in their early 20s and in discussions with them about the value of the forest they often quote sayings that were initiated by the education program. Furthermore, children who are too young to have participated in the education program also quote sayings from the program, which suggests that they are being taught the importance of the forest from their parents, who were influenced by the education program. The importance of advanced training is also now readily apparent. Ten Ugandans have earned or are in the process of earning doctorates in association with our projects. Some of them now are in positions of influence with respect to resource management and education.

In the early 1990s the field station received some of large foreign aid grants, primarily from USAID. The amounts were more than 1500% of any annual budget previously required by the project (Struhsaker, 1997). They induced conflict over spending, very wasteful allocations to structures and items never used, and created resentment among Ugandan participants. This was a time of rapid infrastructural growth, but it was also a period of great waste. Buildings constructed for the field station often cost >10 times going market rates. There was no mechanism established facilitate continued operation after the large foreign aid funds stopped. As a result the period following funding was turbulent and fraught with uncertainty, both for Ugandan and foreign researchers and conservation biologists. Furthermore, the expectations of the local community were not met because they thought that employment would continue following removal of foreign aid. This made conducting small scale conservation activities extremely difficult for many subsequent years and generally led to the field station playing a greatly reduced role in conservation activities relative to its previous role (Oates, 1999).

Some researchers and administrators contended that the funds would have been more appropriately spent and the conservation gains would have been much larger, if the money were used to create a trust fund that would have guaranteed financial support for the field station and protection of Kibale in perpetuity. The funds were sufficient to do this, there was a legal mechanism to facilitate a trust, Ugandan participants asked the donors to establish a trust, but the strategy was not adopted.

WAYS FORWARD: BASIC RESEARCH AND CONSERVATION PERSEVERENCE

Basic Research

After >30 yr of research at Kibale, it is becoming clear that some plant and animal populations exhibit a high degree of natural variation in abundance. Thus, monitoring programs that aim to determine causes of specific variation in abundance will have difficulty separating natural variation from variation resulting from human action. For example, there is evidence that in some areas of Kibale red colobus populations have declined despite excellent protection from hunting and habitat degradation (Chapman *et al.*, 2000; Mitani *et al.*, 2000). Similarly, populations of blue monkeys have declined at 2 undisturbed sites in the park; at one site their numbers in the late 1990s are less than half of what they were in the 1970s (Chapman *et al.*, 2000; Mitani *et al.*, 2000). The decline may be associated with shifts in forest structure and long-term cycles of fruit production. For example, Lwanga *et al.* (2000) recorded a decline in specific richness, diversity, stem number, and basal area in Kibale forest plots monitored during 1975–1980 and in 1997–1998. We have witnessed a consistent decline in the proportion of trees fruiting during the 1970s and 1980s, following by an increase throughout the 1990s (Chapman *et al.*, 2004; Figure 2). The phenological changes may be associated with regional climatic change. Presently, the Kibale region is receiving *ca.* 300 mm more rain than it did at the start of the century, droughts are less frequent, the rainy season is coming earlier, and the average maximum monthly temperature is 3.5°C hotter and the average minimum monthly temperature is 2°C cooler than they were 25 yr ago. With such climatic change, maybe it is not surprising that we have documented changes in phenology and forest structure.

However, finding simple, consistent causes of complex biological phenomena, such as determinants of primate abundance, is unlikely. Instead, several recent elegant studies have highlighted the importance of considering multifactoral explanations. Moreover, population abundance can be regulated by other, nonfood resource-related factors, such as parasitic load and predation. For example, based on a 68-mo study of howlers (*Alouatta palliata*) and a parasitic bot fly (*Alouattamyia baeri*), Milton (1996) concluded that the annual pattern of howler mortality results from a combination of effects including age, physical condition, and larval burden of the parasitized individual, which becomes critical when the population experiences dietary stress (Gulland, 1992). In Kibale, it has been documented that the prevalence and diversity of gastrointestinal parasite infections are substantially greater for red-tailed monkeys in areas that have been

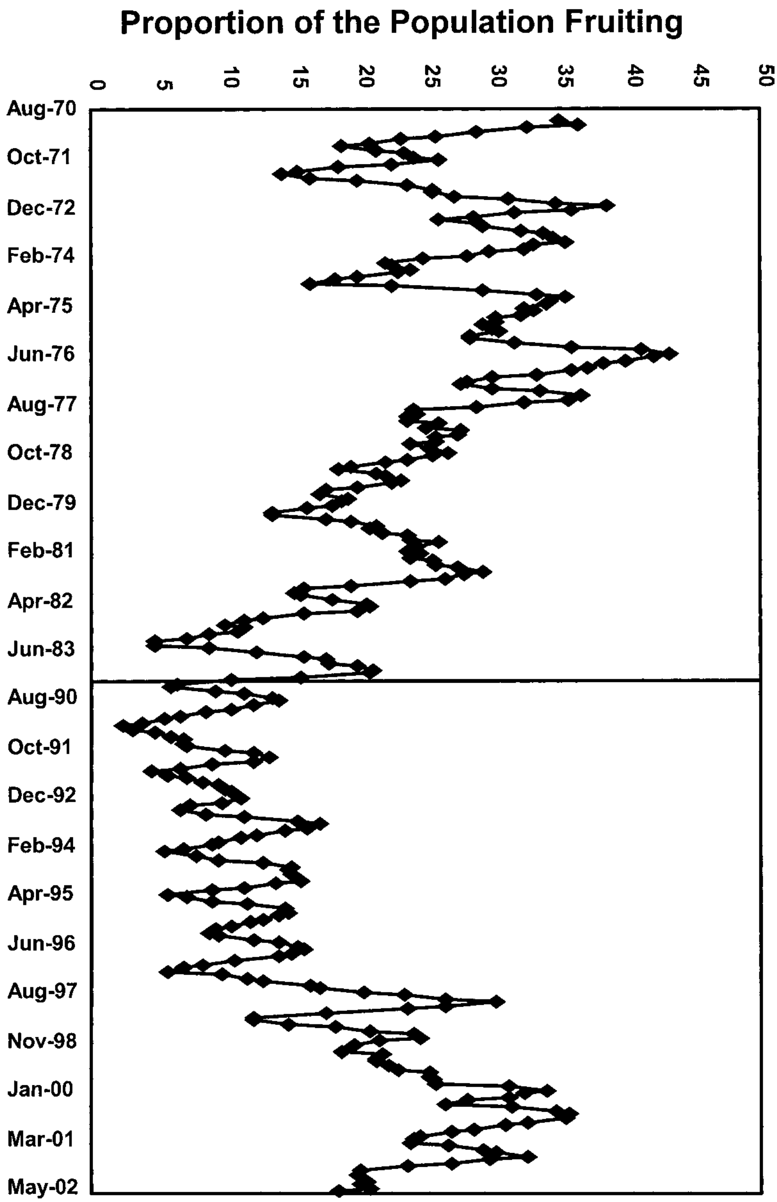

Fig. 2. The 4-mo running average of the proportion of the population fruiting between 1970 and 1984 and 1990 and 2002 in Kibale National Park, Uganda. It includes the following species: *Pouteria altissima, Celtis africana, Celtis durandii, Diospyros abyssinica, Funtumia latifolia, Parinari excelsa, Strombosia scheffleri, Teclea nobilis*, and *Uvariopsis congensis*.

Table I. Mean group densities for primate species in 3 areas (unlogged, lightly logged, and heavily logged) of Kibale National Park, Uganda during 1980–1981 and 1996–1997 census periods. P values based on Kruskal-Wallis test. Tests post-hoc reveal differences between pairs of sites (U = unlogged, L = lightly logged, H = heavily logged). See Chapman *et al.*, (2000) for more detailed presentation of the results

	Group densities (groups/km)^2				
Species	Unlogged	Lightly logged	Heavily logged	*P*	Post-hoc
1980–1981					
Procolobus tephrosceles	5.46	5.78	3.08	0.007	H < L & U
Colobus guereza	0.89	3.31	4.81	<0.001	All sites differ
Cereopithecus ascanius	5.58	7.03	2.21	<0.001	H < L & U
Cercopothecus mitis	2.53	2.06	1.71	0.224	
Lophopithecus albigena	1.04	1.03	0.27	0.142	
1996–1997					
Procolobus tephrosceles	5.50	4.35	4.43	0.265	
Colobus guereza	2.00	4.83	9.12	0.001	All sites differ
Cercopithecus ascanius	4.83	11.48	1.04	<0.001	H < L & U
Cercopithecus mitis	1.00	0.91	0.35	0.304	
Lophocebus albigena	1.13	2.41	0.87	0.065	

Note. The values reported here differ slightly from those in Skorupa 1988 and Struhsaker 1975, 1997. The differences result from recalculating the strip width from the original data. The recalculation was necessary to ensure that the same methods were used to calculate strip width during all 3 time periods.

subjected to logging versus individuals from undisturbed areas (Gillespie and Chapman unpub. data). Furthermore infection risk is greater for primates in logged areas versus those in undisturbed forests, Gillespie and Chapman (unpub. data) evaluated infection risk via modified sedimentation technique to recover infective-stage parasites from leaves collected from the canopy.

Predators, too, can cause severe temporary reduction in population size (Isbell, 1990) and can potentially be an important regulatory force. For example, a single leopard (*Panthera pardus*) might have been responsible for the crash of a mountain gorilla (*Gorilla gorilla beringei*) group in Bwindi, Uganda (Butynski *et al.*, 1990). Watts and Mitani (2002) estimated that chimpanzees at Ngogo in Kibale kill between 6.5 and 12% of the red colobus population annually. The harvest level will significantly influence the population and has probably contributed to the decline in red colobus there (Mitani *et al.*, 2000).

These studies suggest that a profitable approach to provide useful information for conservation planning will be to evaluate the relative contribution of each factor to regulate primate numbers. It is likely that this is very dynamic, with different factors playing important roles only intermittently. For example, with regard to the effects of food over the last 12 yr, temporal variability in fruit availability was high; the proportion of trees per mo with ripe fruit varied from 0.14 to 15.93%. In addition, there was dramatic interannual variation in fruit availability: in 1990, on average only 1.09% of trees bore ripe fruit each month, while in 1999 an average of 6.67% of trees bore fruit each mo. If a month of fruit scarcity is considered as one with less than <1% of monitored trees bearing ripe fruit, there is considerable interannual variation in how often frugivores experienced food shortages. For example, 9 of the 12 mo in 1990 had <1% of the trees with fruit; while in 2000, no mo had <1% of trees fruiting. Over the past 12 yr, fruit has become more available, fruit-scarce months have declined in frequency, and the duration of periods of fruit scarcity has decreased. Similarly, if predators move into the area, predation rates can vary dramatically from one time to the next. For example, Isbell (1990), found that 70% (14) of all vervet (*Cercopithecus aethiops*) deaths were attributable to a 31-day interval when a leopard had established its territory in the area. Likewise, disease is variable in its impact on animal populations (Milton, 1996).

In reality, all 3 factors—food resources, disease, and predation—likely interact synergistically to result in the patterns of variation in abundance. Such variability points both to the importance of long-term monitoring and of novel approaches to evaluate when populations are stressed to tease apart their interactive effects.

Ideas for Effective Park Management

Clearly as scientist we must endeavor to unravel biological complexity. It is also just as clear that the lag time between quantifying biological interactions and implementing conservation tactics in light of the data is typically too great to meet immediate conservation planning needs. Thus, basic research must be conducted against a backdrop of ongoing conservation planning and implementation. Struhsaker (2002) listed 8 requirements for successful conservation programs based in national parks.

1) effective law enforcement;
2) long-term commitment: 20 yr;
3) permanent collaborative associations with international organizations;
4) training and participation of nationals;
5) scientific presence and monitoring;
6) flexible management plans;
7) education and support at both local and national levels; and
8) appropriate level of secure funding (e.g., trust funds).

The guidelines are self-explanatory, thus we will not discuss them in detail. We simply stress the importance of perseverance. Kibale is a relatively intact ecosystem, while other forested areas, even forest reserves and national parks in Africa have largely been converted. While Kibale faces many challenges and there are many ways that the operation can be improved, it is harboring thriving populations of primate, duikers, and elephants. Even species that were hunted to very low numbers, such as leopards, are showing signs of recovery.

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